

COPEPOD SPECIES RICHNESS AS AN INDICATOR OF LONG-TERM CHANGES IN THE COASTAL ECOSYSTEM OF THE NORTHERN CALIFORNIA CURRENT

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ABSTRACT

Since at least the late 1960s, the coastal waters of the northern California Current have been warming 0.08°C per decade (summer) and 0.06°C per decade (winter). Over the same time period, for summers when the Pacific Decadal Oscillation (PDO) was negative and when zooplankton samples were available for study, copepod species richness increased from 6.9 species during 1969–73, to 7.8 from 1999–2002, and 8.9 from 2007–08. During summers when the PDO was positive, species richness increased from 9.1 (1990–92) to 12.2 (2003–06). The trend towards warmer sea surface temperatures and higher species richness suggests that the coastal branch of the northern California Current receives less water from the cold sub-Arctic Pacific Ocean and more water from the subtropical water mass offshore of Oregon. These changes have been accompanied by a reduction in survival of coho salmon (*Oncorhynchus kisutch*) from the 1970s (range of 6%–12%) to an average of 3% over the past decade. Significant correlations between copepod species richness and coho salmon survival suggest that a time series of species richness may be sufficient to create an index for changes in food-chain structure.

INTRODUCTION

The California Current Ecosystem (CCE) is designated as one of eight large marine ecosystems (LMEs) within the U.S. exclusive economic zone. However, the CCE is not a single ecosystem rather it is composed of many connected ecosystems as a result of strong latitudinal and longitudinal gradients in physical forcing and biological response. The northern end of the current is dominated by strong seasonal variability in winds, temperature, upwelling, and plankton biomass, whereas the southern end of the current has much less seasonal variability in these parameters. The northern end of the CCE is usually dominated by sub-arctic boreal fauna whereas the southern end is dominated by tropical and sub-tropical species. The two regions are separated by two faunal boundaries, i.e., regions where changes in species composition are more rapid: in the waters between Cape Blanco, Oregon and Cape Mendocino, California, and in the vicinity of Point Conception, California.

Highly variable and strong climate signals have been observed recently throughout the California Current, which are affecting ecosystem structure. For example, during the past 30 years, the California Current experienced a prolonged warm event (1989–96), the largest El Niño of the past century (1997–98), two strong La Niña events (initiated in 1999 and 2008), a four-year period of strong upwelling, cold ocean conditions and high productivity from 1999–2002 (Peterson and Schwing 2003), and four years of weak upwelling, warm ocean conditions and reduced biological productivity (2003–06). This recent period of warm ocean conditions reached a climax in 2005, when an unusual delay of upwelling from its usual start in April or May to mid-July (Kosro et al. 2006; Pierce et al. 2006) led to an increase in subtropical zooplankton species in the northern California Current (Mackas et al. 2006), declines in zooplankton biomass and a collapse of the food chain (Hooff and Peterson 2006), along with widespread deaths and nesting failure of many seabird species (Sydeman et al. 2006; Parrish et al. 2007). Survival of salmon stocks that went to sea during the spring and summer of 2005 and 2006 became so low that the salmon fishery was closed coast-wide during the summer of 2008. These observed changes in ocean conditions are correlated with the Pacific Decadal Oscillation (PDO) as well, with warm (cold) conditions associated with warm-phases (cold-phases) of the PDO; and cold (warm) phases result in good (poor) salmon survival (Mantua et al. 1997; Peterson and Schwing 2003).

Abrupt changes notwithstanding, ongoing long-term monitoring throughout the California Current suggests that more subtle but measurable changes have taken place in both physical and ecosystem structure over the past 30–40 years. Physical changes include a general warming of the water column and increased water-column stratification (Bograd and Lynn 2003; Huyer et al. 2007; Lavaniegos and Ohman 2007), shoaling of the oxycline, and decreased oxygen concentrations (Chan et al. 2008; Bograd et al. 2008). Biological changes in the southern California Current include decreased biomass of zooplankton (McGowan et al. 1998; although the biomass changes have since been shown to be due to long-term

changes in salp composition by Lavaniegos and Ohman 2007), an increase in the abundance of southern and tropical euphausiid species in the southern California Bight, a decreased abundance of a northern species, *Thysanoessa spinifera* (Brinton and Townsend 2003), and increased abundances of oceanic larval fish in the southern California Current (Hsieh et al. 2005).

For the northern California Current, biological changes include earlier maturation of *Neocalanus plumchrus* C5 off Vancouver Island (Mackas et al. 2007) and Oregon (Liu and Peterson, in press), higher abundances of subtropical copepod species and increased biodiversity of copepods (Hooff and Peterson 2006) off Oregon, highly variable salmon runs (Peterson et al. 2006), increased abundance of sardines (*Sardinops sagax*; Emmett et al. 2005), the first records of spawning by hake (*Merluccius productus*), a fish which normally spawns in the southern California Current (Phillips et al. 2007), and an invasion of the voracious Humboldt squid (*Dosidicus gigas*; Field et al. 2007). Albacore tuna (*Thunnus alalunga*), a fish that populates the North Pacific Ocean subtropical gyre, now occur far closer to shore than during the 1970s and have become a major regional fishery in the Pacific Northwest. Other examples can be gleaned from the annual CalCOFI "State of the California Current Reports" (e.g., McClatchie et al. 2008). Taken as a whole, these changes suggest that the northern California Current is slowly becoming more sub-tropical in nature.

Because of long-term changes in physical and ecosystem structure of the California Current towards a more subtropical ecosystem, and the impacts of recent high frequency variability in physical forcing on lower and upper trophic levels, managers have become increasingly interested in receiving regular and timely updates on ocean conditions. They ask if there are components of the ecosystem that can be monitored easily and if there are ways to report regularly on significant changes in the state of the California Current rather than through the peer-reviewed literature. The purpose of this contribution is to demonstrate that change in zooplankton species composition alone is a good candidate as an indicator of change in ecosystem structure. This is based on Peterson and Schwing (2003) who showed that the Pacific Decadal Oscillation is correlated with the biomass of "northern copepod species" (*Calanus marshallae*, *Pseudocalanus mimus* and *Acartia longiremis*), and that the biomass of these northern species is in turn correlated with coho salmon survival. Moreover, Hooff and Peterson (2006) showed that there was a significant correlation between the monthly value of the PDO and both the monthly averaged sea surface temperature (SST) off Newport, Oregon as well as copepod species richness.

This information is now used to produce outlooks of the success/failures of salmon runs in the Pacific North-

west, one year in advance, and is posted to the Web at <http://www.nwfsc.noaa.gov> (click on "Ocean Index Tools"). Environmental information posted to this site gives managers the opportunity to track both changes in physical oceanographic conditions and food-chain structure in coastal waters of the California Current off the Pacific Northwest. Moreover, similar information is posted quarterly at <http://www.pacoos.org> (click on "PaCOOS Quarterly Update of Climatic and Ecological Conditions in the CA Current LME"), thus allowing managers and others to track changes throughout the broader California Current on a quarterly basis.

Monitoring zooplankton is a quick and easy way to track changes in ocean conditions and food-chain structure in coastal waters because copepods, being planktonic, are indicators not only of the presence or absence of different water masses, but also of changes in food-chain structure. That is, when the PDO is in a negative phase, cold ocean conditions prevail in the northern California Current resulting in a lipid-rich boreal copepod community, whereas when the PDO is in a positive phase, warm ocean conditions are present which result in a lipid-poor subtropical community (Peterson and Hooff 2005; Hooff and Peterson 2006). Such an approach is an extension of the "indicator species concept" pioneered by Johnson and Brinton (1963), whereby we use different species groups as both indicators of the presence or absence of warm- or cold-water types and as indicators of the bioenergetic content of the lower trophic level organisms.

In this paper, time series of copepod biomass and copepod species richness previously published in Peterson and Schwing (2003) and Hooff and Peterson (2006) are updated. These updated time series are used to demonstrate that copepod species richness alone (that is, the number of species in a given plankton sample) is sufficient to track changes in the coastal marine ecosystem off Oregon. Furthermore, it is shown that this simple index of ecosystem structure is significantly correlated with the survival of coho salmon which may be useful for salmon managers.

METHODS

The historical data sets upon which this paper is based are derived from sampling along the Newport Hydrographic Line for hydrography (monthly to bimonthly, 1961–72; Huyer et al. 2007), and for zooplankton (sampled biweekly-monthly 1969–73; 1977, 1978, 1983 and 1990–92; Peterson and Miller 1975; Hooff and Peterson 2006). More recent data are from biweekly cruises off Newport, which were initiated in 1996. Historical hydrographic data are derived from water sampling at 10 m intervals throughout the water column using Nansen bottles equipped with reversing thermometers. No hy-

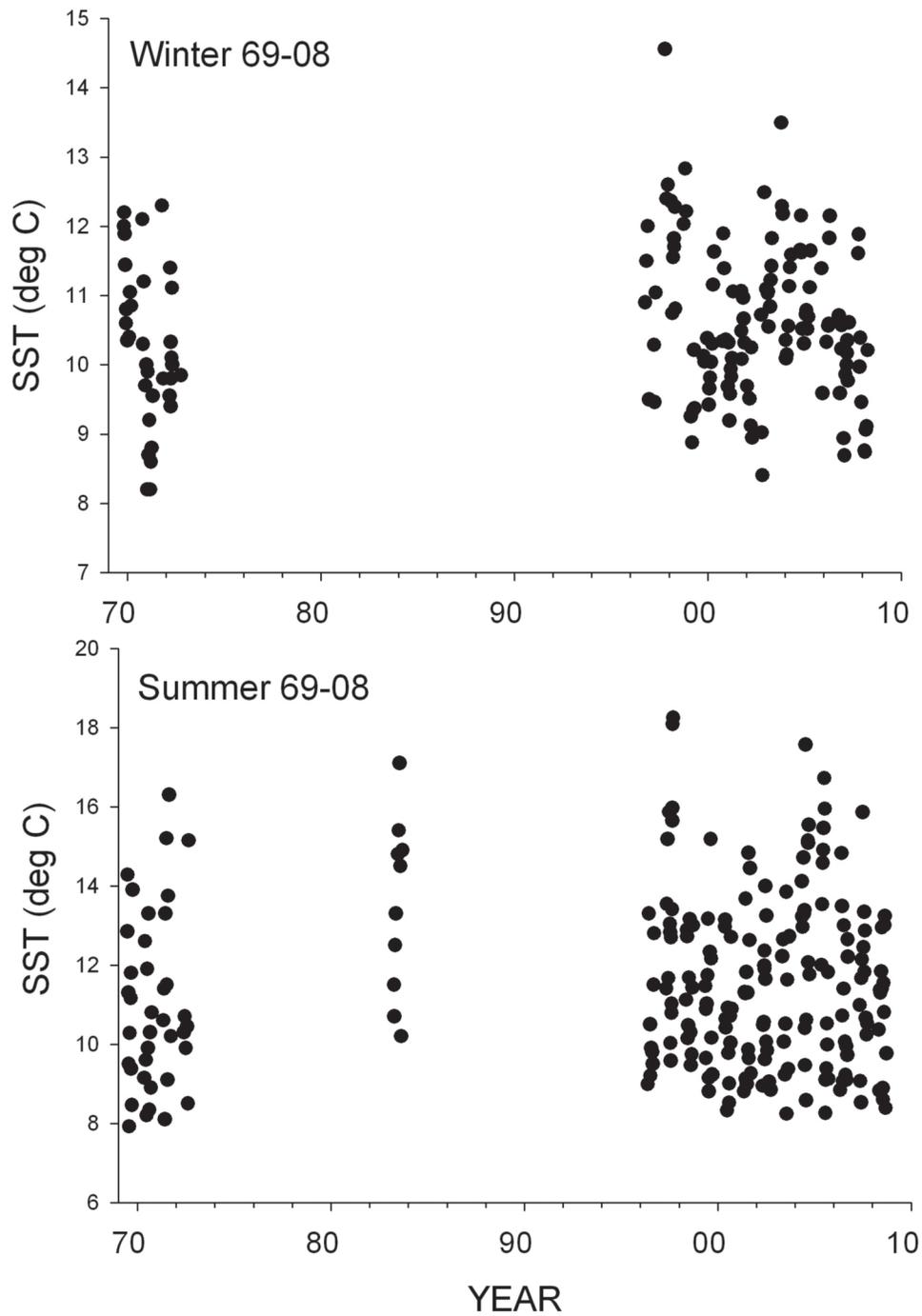


Figure 1. Sea surface temperature at station NH 05 from 1969–73, 1983 and 1996–2008.

drographic data are available for 1977, 1978, or 1990–92. Recent hydrographic measurements were made with a SeaBird SBE 19+ as water-column profiles of temperature and conductivity. Zooplankton was collected with several types of plankton nets over the past forty years: during 1969–73, 1977, 1978 and 1983, the zooplankton was sampled with a 20 cm Bongo net fitted with 240

μm plankton nets and a TSK flowmeter, towed in a step-oblique manner from near the sea floor to the sea surface. In 1990–92 the zooplankton was sampled with a 0.75 m diameter net fitted with a 333 μm net and a TSK flow meter, towed vertically throughout the water column. From 1996 to the present, sampling was with a 0.5 m diameter 202 μm mesh net with a TSK flowmeter,

hauled vertically from a few meters off the sea floor to the surface. All of the data shown in this paper are from a single station, referred to as NH 05, located five miles offshore along the Newport Hydrographic (NH) line in 62 m water depth. The station location can be found in recent CalCOFI Reports (e.g., Peterson et al. 2006b; McClatchie et al. 2008). Data from 435 zooplankton samples are presented.

To enumerate the zooplankton, each sample was first rinsed with freshwater, then poured into a graduated cylinder and allowed to settle for at least 30 minutes; then the sample was poured into a beaker and diluted to 5–10 times the settled volume. Subsamples were then taken with a 1 ml piston pipette and all copepods were enumerated by species and developmental stage. At least two subsamples were enumerated (but up to four or five subsamples for those samples with small volumes of plankton) such that a total of at least 400 individuals were enumerated in all subsamples combined. Usually each subsample contained 200–400 individuals. All of the samples were enumerated by the same person (W. Peterson) except for the 1983 samples which were enumerated by another expert (C. Miller) who mentored the other sampler, thus there is not likely to be any differences in the species identifications. All data were entered into a Microsoft Access database; all analyses and plots were done using Sigma Plot 10.0. Species richness is defined here simply as the estimated number of species in a sample.

Other data shown in this paper include the Pacific Decadal Oscillation time series, which is from <http://jisao.washington.edu/pdo/PDO.latest>, and the time series of coho salmon survival from the Pacific Fisheries Management Council Web site. Members of the Salmon Technical Committee of the Pacific Fisheries Management Council calculated survival data from estimates of the number of salmon released by hatcheries in southwest Washington and northern Oregon and from estimates of the number of salmon caught in the fishery the following year plus the number of salmon that return to the hatcheries and streams to spawn (see Logerwell et al. 2003). The ratio of salmon accounted for in year +1 to salmon released from hatcheries in year 0 is the survival rate. Since most of the marine mortality of coho salmon happens during the first summer at sea (Pearcy 1992), regressions of coho salmon survival with environmental covariates (e.g., copepod species richness) were constructed using the coho survival data lagged by one year.

RESULTS

Figure 1 shows the time series of SST at NH 05 for all data. The range in values was typically 8°–12°C during the winters of 1969–73 but slightly warmer in 1997–2008, at 8.5°–13°C. The range in summer values

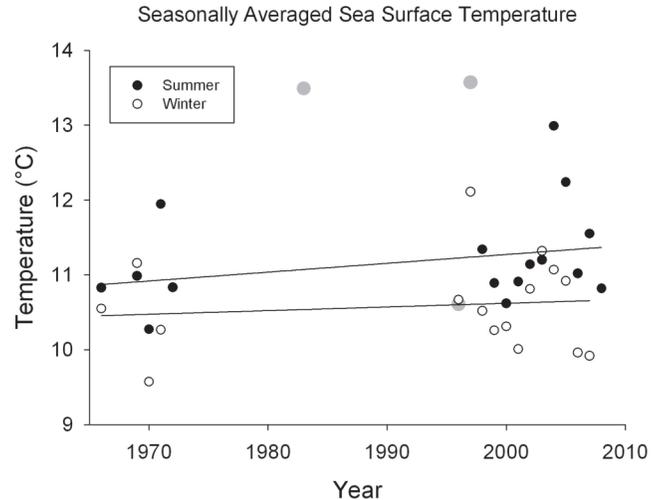


Figure 2. Seasonally-averaged SST at NH 05, for summer (May–September) and winter (October–April). The grey dots are average SST from the two El Niño years, 1983 and 1997. SST was anomalously high during those years; neither was included in the regression analysis. Although neither regression line was significantly different from zero (due largely to the very slight changes in temperature with time), the slopes (indicating the rates of change) are similar to those from the long-term historical records of global SST (see tab. 1).

TABLE 1
Rates of change of sea surface temperature (SST) and at a depth of 50 m at station NH 05 compared to rates of change of global SST, based on summer- (May–September) and winter- (October–April) averaged SST (Newport) and from data shown in IPCC-AR4.

	Deg C per decade	Deg C per 40 years (since 1960s)
All data (summer)	0.078	0.31
All data (winter)	0.056	0.23
Summer average SST	0.118	0.53
Winter average SST	0.049	0.02
Summer T at 50 m depth	0.108	0.43
Winter T at 50 m depth	–0.011	no data
Global Ocean SST	0.18	0.72
Line P SST	0.19	0.76

was 8°–16°C during 1969–73 but slightly warmer during 1997–2008 at 8.2°–17°C. Figure 2 shows the seasonally-averaged values from the same data set for summer (May–September) and winter (October–April). This Figure illustrates that winter and summer averages from the 1960s and 1970s were slightly cooler than recent measurements.

Regression analysis of SST with time did not reveal that the slope of the trend was significantly different from zero ($p = 0.33$), however, the slopes of the lines were similar to the slope of the trend in global SST reported by the IPCC-AR4 (tab. 1). When all data from NH 05 were combined and analyzed, the overall increase in temperature from 1969 to 2008 (a span of 40 years) was 0.23°C (winter) and 0.31°C (summer). A slightly dif-

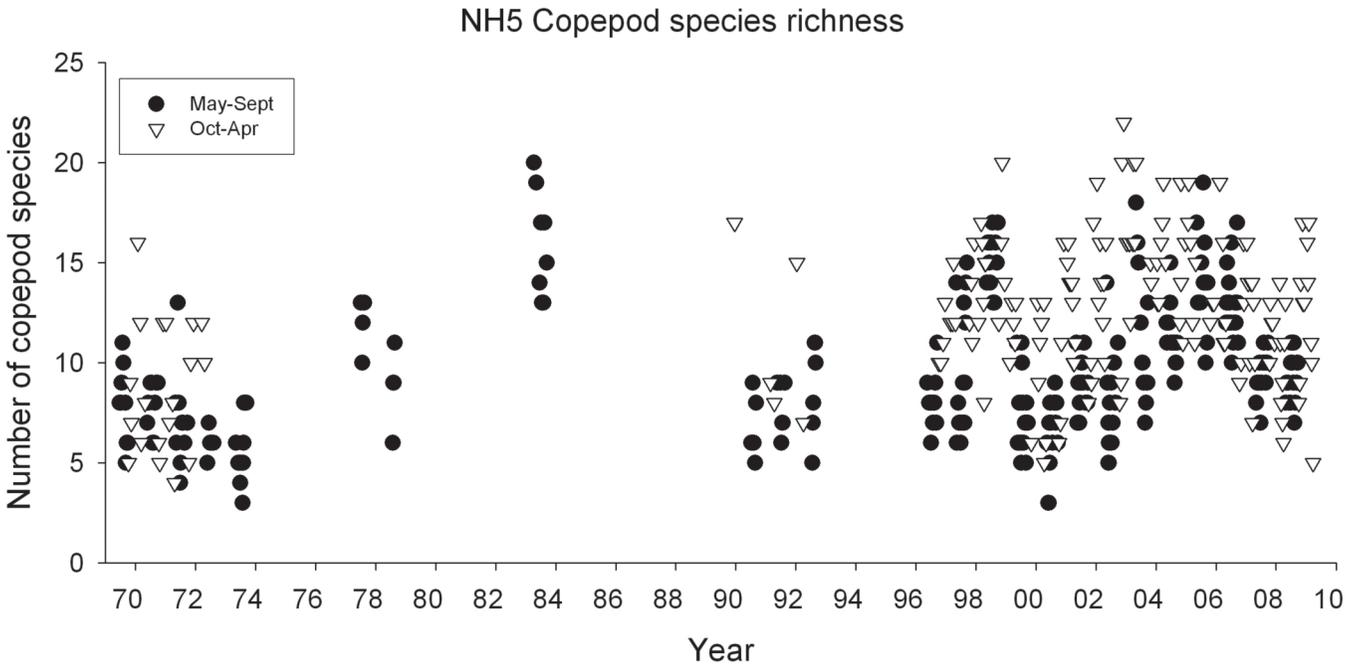


Figure 3. Number of copepod species in zooplankton samples collected at station NH 05, five miles off Newport Oregon, from 1969–73, 1977, 1978, 1983, 1990–92, and 1996–2008. The regression of the number of species on year was significant ($p < 0.001$) but explained only 15% (adjusted R -sq) of the variance. The equation was $y = -0.58 + 0.0003x$. The slope of 0.0003 species per day is equivalent to an increase of 4.38 species over the 40-year time series. Slopes from regressions for summer and winter analyzed separately were the same (4.4 species in 40 years). Data from the 1983 El Niño were excluded from this analysis.

ferent result was obtained when the seasonally-averaged values (summer = May–September; winter = October–April) were regressed one year. This analysis showed that seasonally-averaged SST values at NH 05 have been increasing at a rate of 0.118°C per decade since 1969 during summer, but half that rate in winter at 0.049°C per decade. Similarly, the near-bottom waters at NH 05 in summer have warmed at a rate of 0.108°C per decade but are virtually unchanged in winter at a rate of -0.011°C per decade (tab. 1).

The number of copepod species collected in plankton samples has increased since the first sampling in 1969. Figure 3 shows data collected during 1969–73, 1977, 1978, 1983, 1990–92, and 1996–2008 and although the time series is not continuous, a general increase in species richness is clear. The regression of the number of species on year was significant ($p < 0.001$) but explained only 15% (adjusted R -sq) of the variance. The equation was $y = -0.58 + 0.0003x$. The slope of 0.0003 species per day is equivalent to an increase of 4.4 species over the 40-year time series. Slopes from regressions for summer and winter analyzed separately yielded the same result (4.4 species added over the 40-year period). Data from the 1983 El Niño were excluded from this analysis.

A slightly different result was seen when the number of species were first averaged by season then plotted against year (fig. 4). The regressions were significant (winter = 0.133 species per year; $p = 0.002$; adj. R -sq = 0.52; summer = 0.082 species per year; $p = 0.017$, adj. R -sq = 0.22). The slopes of the regressions were equivalent to adding 5.3 species to the copepod community in 40 years (winter) and 3.3 species to the community in 40 years (summer). The data from the 1983 El Niño event were again excluded from the regression.

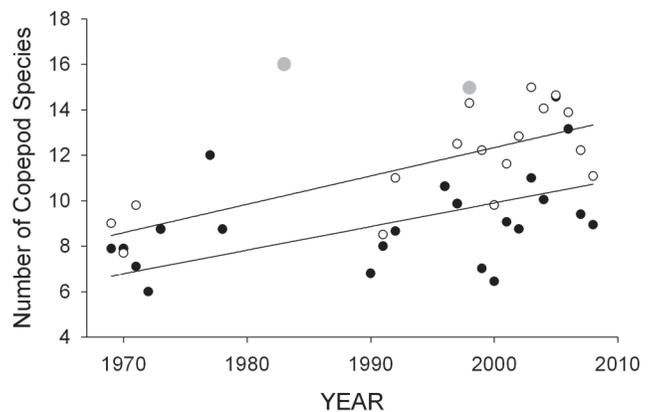


Figure 4. Number of copepod species collected in zooplankton net samples at station NH 05, off Newport, Oregon, plotted against year, for data averaged for summer months (May–September, solid circles) and winter months (October–April, open circles). Regressions were highly significant: winter = 0.133 species per year ($p = 0.002$; adj. R -sq = 0.52); summer = 0.082 species per year ($p = 0.017$, adj. R -sq = 0.22). Slopes of the line are equivalent to 5.3 species in 40 years (winter) and 3.3 species in 40 years (summer). The grey data points are from the 1983 and 1997 El Niño events, and were excluded from the regression.

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Interannual differences in species richness were correlated with the Pacific Decadal Oscillation (fig. 5).

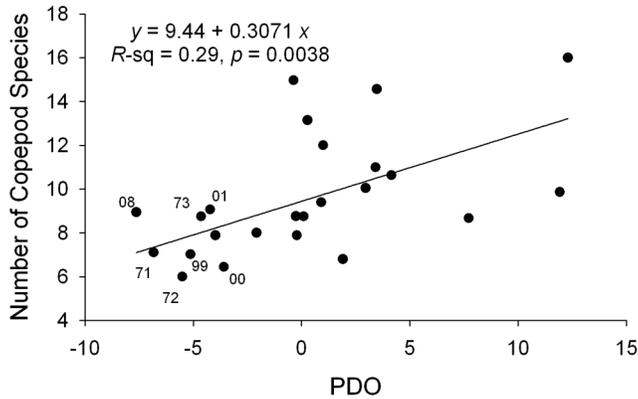


Figure 5. Scattergram showing the relationship between copepod species richness and the Pacific Decadal Oscillation (PDO) during summer months. A warm phase of the PDO results in more species being found at station NH 05, a cool phase, fewer species. Year is identified for those summers when the PDO was strongly negative to illustrate the high diversity observed in 2008 when the PDO had the most negative of all years sampled.

During the warm phase of the PDO, more species are found, whereas during the cool phase, fewer species occur. However the PDO accounts for only 30% of the variance, thus other factors contribute to the increase in copepod species richness. The correlation with the PDO must be examined with some caution (especially since less than one-third of the variance in species richness is explained) because during the summer of 2008, for example, the PDO was strongly negative yet species richness was relatively high during that summer (8.9 species) compared to the 1970s (average of 6.9 species from 1969–73, tab. 2). The species which occur most frequently during summers include *Calanus marshallae*, *Pseudocalanus mimus*, *Centropages abdominalis*, *Acartia longiremis* and *Oithona similis*. Recently other “northern” species have occurred more frequently during the summers of 2007 and 2008 as compared to 1969–73, including *Tortanus discaudatus* (17% of samples in 2007–08 vs. 5% of samples from 1969–73), *Metridia pacifica* (62% vs. 47%), and *Microcalanus pusillus* (38% vs. 23%) and *Acartia hudsonica* (86% vs. 74%). Each of these is a sub-arctic species which might suggest a greater influx of sub-arctic water into the northern California Current (NCC) during 2007, and especially 2008 when the PDO was extraordinarily negative. Since *M. pacifica* and *M. pusillus* are boreal oceanic species, whereas *T. discaudatus* and *A. hudsonica* boreal neritic, this suggests that increased volumes of subarctic water entered the NCC, from both an offshore source as well as along a coastal corridor.

Similarly, the number of species observed during the warm phase of the PDO in summers of 2003–06 (average of 12.2 species for an average PDO score of 2.54) was far more than during the warm phase of the PDO in 1990–92 (9.1 species for a higher PDO score of 3.26). In this case, the species with a greater frequency of occur-

TABLE 2
 Number of copepod species in zooplankton samples collected off Newport, Oregon, averaged for summer (May–September) and winter (October–April) months.

Year	Summer	Winter
1969	7.89	9.00
1970	7.89	7.70
1971	7.10	9.80
1972	6.00	
1973	5.50	
1977	12.00	
1978	8.75	
1983	16.00	
1990	6.80	
1991	8.00	8.50
1992	8.67	11.00
1996	10.63	
1997	9.87	12.50
1998	14.97	14.29
1999	7.02	12.22
2000	6.45	9.81
2001	9.07	11.62
2002	8.76	12.83
2003	11.00	14.98
2004	10.05	14.06
2005	14.50	14.64
2006	13.15	13.89
2007	9.40	12.21
2008	8.94	11.08

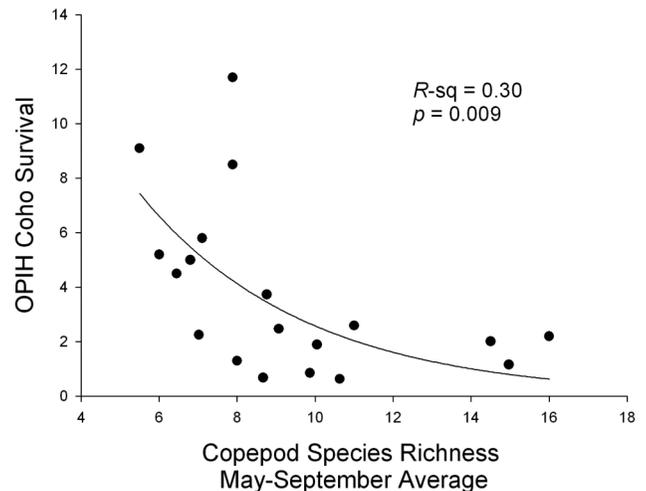


Figure 6. Relationship between survival of hatchery-raised coho salmon and copepod species richness. The plot compares data from the summer that the fish entered the ocean. Coho return to their natal streams/hatcheries 18 months after entering the sea.

rence during 2003–06 were *Clausocalanus pergens*, *C. parapergens* and *C. arcuicornis*, whereas none were observed during 1990–92, and *Paracalanus parvus* (12.5% in 1990–92 vs. 98.3% in 2003–06). Thus, despite the positive correlation with the PDO, the increasing number of species with time, especially over the past 10 years, is explained only in part by the PDO.

Finally, interannual differences in copepod species richness were significantly correlated with survival of coho salmon (fig. 6).

DISCUSSION

The surface waters of the coastal northern California Current are warming at a rate of about 0.08°C per decade (in summer) and 0.06°C (in winter). These rates are about one-half the rate of the southern Gulf of Alaska (0.19°C; Crawford et al. 2007) and that of global SST (0.18°C; Domingues et al. 2008). Although the trends in temperature vs. time in the NCC, the Gulf of Alaska, and globally are not statistically significant (due largely to the strong seasonal cycle in temperature), few scientists doubt that the warming trend is real. The slower rate at which the northern California Current is warming compared to global SST is likely related to the influence of coastal upwelling on summer temperatures. Both the Gulf of Alaska and global temperatures are more a function of solar heating whereas coastal waters of the NCC are kept somewhat cooler by upwelling. The observation that coastal waters are warmer now than in the 1970s suggests that coastal upwelling is less intense, however this does not appear to be the case because there is no difference in upwelling at 45°N since at least 1969 (the slope of the linear regression was 0.81 upwelling units per year, but the slope was not different from zero; $p = 0.33$; not illustrated). This clearly does not meet expectations of increased upwelling (Bakun 1990; Snyder et al. 2003) expected with global warming, at least for the waters off central Oregon.

Temperature trends in the CalCOFI region of the southern California Current are similar to the global trend. Bograd and Lynn (2003) found a warming trend of about +1°C since 1950 (equivalent to 0.2°C per decade, the same rate as in the Gulf of Alaska). DiLorenzo et al. (2005) also reported on the same CalCOFI hydrographic data set and found not only a warming of SST by 1.3°C, but a deepening of the thermocline by 18 m, and increased stratification over the period 1950–99. Moreover, through use of a ROMS (Regional Ocean Modeling System), they showed that increased stratification associated with warming reduces the efficiency of coastal upwelling in bringing cold waters up to the sea surface. This in turn has resulted in lesser amounts of nutrients being brought to the sea surface and lower productivity, processes which they suggest may explain the order of magnitude declines in zooplankton biomass in the CalCOFI region (but see Lavaniegos and Ohman 2007 for an alternate view).

Most of the variation in both temperature and copepod species richness in coastal waters off Newport, Oregon, was at the seasonal time scale. These variations are driven by the seasonal cycle in the winds, circulation and coastal upwelling. During the summer, coastal winds blow from the north, causing upwelling along the Washington and Oregon shelf. Shelf waters of Washington and Oregon are cold and salty at this time of the year

and boreal copepods are transported along the shelf from a northern source (Peterson and Miller 1975). During winter months, winds are from the southwest, causing seasonal downwelling and coastal currents are northward. Shelf waters are warmer and fresher than in summer as a result of the Davidson Current transporting water from the south and from offshore, bringing with it subtropical copepods from shelf waters off California as well as from subtropical waters which lie offshore of Oregon (Peterson 1972; Morgan et al. 2003).

At the decadal time scale, some of the variability in summer-time species richness is explained by the PDO (which accounted for 30% of the variance). However, given that the gradual increase in species richness since the 1970s broadly matches the general warming of coastal waters of the northern California Current, a hypothesis could be offered that the increased warming and increased species richness are both linked to global warming. But what mechanism would link warming with species richness? As discussed by Hooff and Peterson (2006), one potential (and testable) mechanism that results in an increased number of species is related to the source waters which feed the coastal waters off Oregon. If the source waters which feed the coastal currents include the transport of a greater volume of water from offshore of Oregon, which is subtropical in nature, and which has species richness values on the order of 15–20 species in a zooplankton sample (Keister and Peterson 2003; Peterson unpub. data), then increased species richness in coastal waters would result. Indeed, ROMS studies conducted by Chhak and DiLorenzo (2007) and Keister et al.¹ (in prep) demonstrate that it is the on-shore movement of surface waters from offshore Oregon during a positive phase of the PDO that results in increased species richness. This is consistent with conclusions drawn by Hooff and Peterson (2006) who suggested that changes in source waters driven by remote basin-scale forcing, not local environmental events, cause interannual-to-decadal variations in copepod biodiversity in the northern California Current.

The results of the ROMS study by the DiLorenzo group is supported by observations reported by Parrish et al. (2000). They showed that surface waters entering the California Current during 1976–90 (the positive PDO phase) were of sub-tropical origin, due to increased strength of westerly winds. They suggested that remotely-forced variations in surface transport controlled the source and character of the surface waters of the California Current system.

Increased species diversity off Oregon is consistent

¹Keister, J. E., C. A. Morgan, N. Mariani, V. Combes, E. DiLorenzo, and W. T. Peterson. In prep. Copepod species composition linked to ocean transport in the northern California Current. University of Washington. School of Oceanography, Box 357940, Seattle, Washington 98195.

with a prediction from global climate models that the distributions of plants and animals will shift northward. Under this expectation, copepod species richness at one geographic point, such as the Oregon coast, should increase simply because of northward shifts in distribution of sub-tropical species. Indeed, this has been observed in the Gulf of Alaska zooplankton from continuous plankton recorder surveys (Mackas et al. 2007) and from our own unpublished work off Oregon (Liu and Peterson, in press), where we've seen that *Neocalanus plumchrus* have been awakening from diapause earlier and are developing faster, and both are correlated with increased temperature. Thus, the overall conclusion is that the northern California Current is gradually becoming more subtropical in nature, albeit at a slow pace, but especially so when the PDO is in a positive phase. Thus, the observed increase in species richness is likely due to a general warming in the coastal zone of the California Current resulting from both a northward and onshore shift in the distributions of copepod species.

The significant correlation of copepod species richness with coho salmon survival matches the high correlation between the biomass of northern copepod species and coho salmon shown by Peterson and Schwing (2003) and by Peterson et al. (2006a) (see "Ocean Index Tools" at <http://www.nwfsc.noaa.gov>). This suggests that even a very simple index like the number of copepod species in a plankton net sample may be a good proxy index for the "quality" of the food chain in the same manner as suggested by Hooff and Peterson (2006). That is, northern copepods are lipid-rich species (dominated by *Calanus marshallae* and *Pseudocalanus mimus*) whereas southern copepods (dominated by *Calanus pacificus*, *Paracalanus parvus*, *Clausocalanus* spp., *Calocalanus styliremis*, *Ctenocalanus vanus* and *Corycaeus anglicus*) are relatively lipid-poor species. Thus the food chain is anchored by copepods with high-energy density during cold ocean conditions and negative phases of the PDO, whereas the food chain is anchored by copepods with low-energy density during warm ocean conditions and positive phases of the PDO. Biodiversity also changes with the sign of the PDO; as shown in Figure 5, cold conditions have fewer copepod species and warm conditions have a greater number of species. Thus, others working in the California Current may be able to investigate relationships between zooplankton, food-chain structure and fish recruitment simply by enumerating the species in a set of plankton net subsamples, rather than by taking on the far more time-consuming task of carefully enumerating by species and developmental stage. Clearly, the latter would be preferred, but the simpler approach advocated here would add value to any plankton collection. This conclusion is supported by Lavaniegos and Ohman (2007) who noted that measures of biomass are insensitive indicators of cli-

mate forcing; the more compelling data sets (and those most associated with climate-change signals) are changes in species composition.

In conclusion, surface waters of the coastal northern California Current are warming at a rate of about 0.08°C per decade in the summer and 0.06°C per decade in the winter. At the same time, for those years when the PDO was negative, copepod species richness increased from an average of 6.9 species during 1969–73, to 7.8 from 1999–2002, and to 8.9 from 2007–08. Likewise during summers when the PDO was positive, species richness increased from 9.1 (1990–92) to 12.2 (2003–06). Significant correlations between species richness and coho salmon survival suggest that this simple measure of copepod community structure is sufficient to index the changes in food-chain structure suggested by Hooff and Peterson (2006).

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